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Spatial heterogeneity in species composition constrains plant community responses to herbivory and fertilisation

Dorothee Hodapp
Helmholtz Institute for Functional Marine Biodiversity (HIFMB)

Lori A. Biederman
Iowa State University, lbied@iastate.edu

Philip A. Fay
U.S. Department of Agriculture

et al.

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LETTER

Spatial heterogeneity in species composition constrains plant community responses to herbivory and fertilisation

Dorothee Hodapp,[1]* Elizabeth T. Borer,[2] W. Stanley Harpole,[3,4,5] Eric M. Lind,[2] Eric W. Seabloom,[2] Peter B. Adler,[6] Juan Alberti,[7] Carlos A. Arnillas,[8] Jonathan D. Bakker,[9] Lori Biederman,[10] Marc Cadotte,[11] Elsa E. Cleland,[12] Scott Collins,[13] Philip A. Fay,[14] Jennifer Firn,[15] Nicole Hagenah,[16] Yann Hautier,[17] Oscar Iribarne,[9] Johannes M. H. Knops,[18] Rebecca L. McCulley,[19] Andrew MacDougall,[20] Joslin L. Moore,[21] John W. Morgan,[22] Brent Mortensen,[23] Kimberly J. La Pierre,[24] Anita C. Risch,[25] Martin Schütz,[25] Pablo Peri,[26] Carly J. Stevens,[27] Justin Wright[28] and Helmut Hillebrand[1,29]

Abstract

Environmental change can result in substantial shifts in community composition. The associated immigration and extinction events are likely constrained by the spatial distribution of species. Still, studies on environmental change typically quantify biotic responses at single spatial (time series within a single plot) or temporal (spatial beta diversity at single time points) scales, ignoring their potential interdependence. Here, we use data from a global network of grassland experiments to determine how turnover responses to two major forms of environmental change – fertilisation and herbivore loss – are affected by species pool size and spatial compositional heterogeneity. Fertilisation led to higher rates of local extinction, whereas turnover in herbivore exclusion plots was driven by species replacement. Overall, sites with more spatially heterogeneous composition showed significantly higher rates of annual turnover, independent of species pool size and treatment. Taking into account spatial biodiversity aspects will therefore improve our understanding of consequences of global and anthropogenic change on community dynamics.

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[1]*Helmholtz Institute for Functional Marine Biodiversity (HIFMB), Ammerländer Heerstr. 231, 26129 Oldenburg, Germany*
[2]*Department of Ecology, Evolution, and Behavior, University of Minnesota, 1479 Gortner Ave, St Paul, MN 55108, USA*
[3]*Department of Physiological Diversity, Helmholtz Center for Environmental Research – UFZ, Permoserstrasse 15, 04318 Leipzig, Germany*
[4]*German Centre for Integrative Biodiversity Research (iDiv), Deutscher Platz 5e, 04103 Leipzig, Germany*
[5]*Martin Luther University Halle-Wittenberg, Am Kirchtor 1, 06108, Halle (Saale), Germany*
[6]*Department of Wildland Resources and the Ecology Center, Utah State University, 5230 Old Main, Logan UT 84322, USA*
[7]*Instituto de Investigaciones Marinas y Costeras (IIMyC; UNMDP-CONICET), CC 1260, B7600WAG, Mar del Plata, Argentina*
[8]*Department of Physical and Environmental Sciences, University of Toronto at Scarborough, 1265 Military Trail, Scarborough, ON M1C 1A4, Canada*
[9]*School of Environmental and Forest Sciences, University of Washington, Box 354115, Seattle, WA 98195-4115, USA*
[10]*Department of Ecology, Evolution, and Organismal Biology, Iowa State University, 251 Bessey Hall, Ames, IA 50011, USA*
[11]*Department of Biological Sciences, University of Toronto-Scarborough, 1265 Military Trail, Toronto, ON M1C 1A4, Canada*
[12]*Ecology Behavior & Evolution Section, Division of Biological Sciences, University of California San Diego, La Jolla, CA 92103, USA*
[13]*Department of Biology, University of New Mexico, Albuquerque, NM 87131, USA*
[14]*USDA-ARS Grassland, Soil, and Water Lab, 808 E. Blackland Road, Temple, TX 76502, USA*
[15]*Queensland University of Technology (QUT), School of Earth, Environmental and Biological Sciences, Science and Engineering Faculty, Brisbane, QLD 4001, Australia*
[16]*Department of Zoology and Entomology, Mammal Research Institute, University of Pretoria, Pretoria, South Africa*
[17]*Ecology and Biodiversity Group, Department of Biology, Utrecht University, Padualaan 8, 3584 CH, Utrecht, The Netherlands*
[18]*School of Biological Sciences, University of Nebraska, Lincoln, NE 68588, USA*
[19]*Department of Plant & Soil Sciences, University of Kentucky, Lexington, KY 40546-0091, USA*
[20]*Department of Integrative Biology, University of Guelph, Guelph, ON, N1G 2W1, Canada*
[21]*School of Biological Sciences, Monash University, Clayton Campus, VIC 3800, Australia*
[22]*Department of Ecology, Environment and Evolution, La Trobe University, Bundoora 3083, Victoria, Australia*
[23]*Department of Biology, Benedictine College, 1020 North 2nd Street, Atchison, KS 66002, USA*
[24]*Smithsonian Environmental Research Center, 647 Contees Wharf Road, Edgewater, MD 21307, USA*
[25]*Swiss Federal Institute for Forest, Snow and Landscape Research WSL, Zuercherstrasse 111, 8903 Birmensdorf, Switzerland*
[26]*Department of Forestry, Agriculture and Water, Southern Patagonia National University-INTA-CONICET, CC 332 (CP 9400), Río Gallegos, Santa Cruz, Patagonia, Argentina*
[27]*Lancaster Environment Centre, Lancaster University, Lancaster LA1 4YQ, UK*
[28]*Department of Biology, Duke University, Durham, NC 27708, USA*
[29]*Plankton Ecology Lab, Institute for Chemistry and Biology of the Marine Environment, Carl von Ossietzky University Oldenburg, Schleusenstr. 1, 26382 Wilhelmshaven, Germany*
**Correspondence: E-mail: dorothee.hodapp@hifmb.de*

INTRODUCTION

Global warming, increased nutrient input, and habitat fragmentation require species to either adapt, disperse or go extinct. The consequences can be major shifts in species composition (Walther *et al*. 2002; Feeley *et al*. 2011; Moritz & Agudo 2013), high rates of temporal species turnover (Hillebrand *et al*. 2010; Larson *et al*. 2016), increased biological invasions (Seabloom *et al*. 2013, 2015) and species loss (Brook *et al*. 2008; Pimm *et al*. 2014). Depending on the balance of colonisations and extinctions, these compositional changes may or may not result in changes in species number (Hillebrand *et al*. 2010; Dornelas *et al*. 2014; Elahi *et al*. 2015). Understanding species temporal turnover, and identifying its drivers and dependencies will help to interpret the substantial differences in compositional changes observed across communities in response to similar environmental alterations (Jackson & Sax 2009; Avolio *et al*. 2015; Hillebrand *et al*. 2017). Ultimately, it will also provide more reliable predictions of the functional consequences of environmental changes (Fox & Kerr 2012).

While existing community theory can guide our expectations for compositional changes, we need empirical tests to determine their relevance for predicting turnover in response to global change. Temporal turnover can reflect changes in the relative abundance of persisting species as well as the immigration and local extinction of species (Smith *et al*. 2009). Changes in the relative abundances of species reflect internal shifts in dominance, while immigration and replacement of species involve changes in species identity and require the presence of additional species in the regional species pool. Large species pools can be the result of heterogeneous environmental conditions in space and time (Chesson 2000; Holyoak *et al*. 2005). Such conditions provide highly variable niche space and are therefore likely to promote the coexistence of higher numbers of species as well as more distinct local communities (Horn & Mac Arthur 1972). In addition, high degrees of local specialisation of species in heterogeneous landscapes, along with mechanisms such as dispersal limitation (Pinto & MacDougall 2010), can result in potentially higher turnover rates under changing environmental conditions. Thus, temporal shifts in species composition in general, and more specifically in response to environmental changes, are intrinsically related to spatial beta diversity (Adler *et al*. 2005; Korhonen *et al*. 2010; Stegen *et al*. 2013). Here, we refer to compositional changes over time as 'temporal turnover', whereas we use the term 'beta diversity' only to denote compositional differences of communities in space.

While it is commonly acknowledged that spatial context can affect temporal shifts in composition, global change experiments typically analyse data from single plots ignoring all spatial interactions between the plots and their surroundings. In addition, the primary data feeding into synthesis studies on biodiversity responses to global change (Walker & Wahren 2006; Hillebrand *et al*. 2007; Murphy & Romanuk 2014) focus on diversity estimates at the plot scale, treating replicate plots as independent units sampled from a homogeneous landscape. These approaches ignore possible effects of the regional species pool on the changes in species composition in response to treatment application or at least assume that these effects are negligible (Seabloom *et al*. 2015; Harpole *et al*. 2016). Compositional responses to changing environmental conditions might be limited if low beta diversity reduces rates of immigration and consequently constrains temporal turnover. Thus, differences in the magnitude of the biodiversity response between studies, systems, or organism groups might not only reflect differing impacts of drivers, but also varying abilities to respond due to the spatial species distribution of the surroundings (Collins *et al*. 2018). This makes direct comparison of compositional responses to environmental change difficult.

In addition, many common turnover measures share two inconvenient properties: (1) the sensitivity to overall species richness (Rice & Belland 1982) and (2) the inability to distinguish between community turnover caused by changes in species number as opposed to replacement of species (Baselga 2007). Both components contribute to overall turnover measures, but can result from rather different phenomena. While changes in species richness might reflect non-random processes of species loss caused by altered environmental conditions, species replacement can be the consequence of mechanisms such as environmental sorting or successional gradients. Baselga (2010) introduced an approach to separate these two components.

Here, we apply his approach to data from a globally replicated nutrient addition and herbivore exclusion experiment. We then use structural equation modelling to test the following three hypotheses: (1) Beta diversity is determined by site-specific environmental conditions such as spatial and temporal environmental variability. And, (2) increased beta diversity increases the rate of temporal turnover of communities in response to manipulated resource and consumer conditions. Using marginal generalised linear models, we further test the hypothesis that (3) directional shifts in community composition in response to an experimentally altered resource and consumer environment increase with increasing site-level beta diversity. Our analyses reveal that the initial spatial heterogeneity of species composition strongly affects the strength of community responses to changing environments.

MATERIAL AND METHODS

The data used in this study were collected as part of the Nutrient Network (www.nutnet.org), a globally distributed replicated grassland experiment. Manipulations include nutrient supply via addition of nitrogen (N), phosphorus (P), and potassium and micronutrients (K+) and the exclusion of vertebrate herbivores via fencing (see Borer *et al*. 2014a for more details). All treatments were applied to 5×5 m^2 plots using a completely randomised block design. Each site consisted of at least three (maximum six) blocks of 10 plots each. For our analyses, we included data from all sites with measurements of at least 4 years (one pre-treatment year plus 3–5 years of treatment application) which amounted to 41 sites (131 experimental blocks). We focused on temporal turnover in treatment plots. This allowed us to test the responses to the addition of all major nutrients and herbivore exclusion, that is, untreated controls (Ctrl), plots fertilised with all three major nutrients (NPK), plots without grazers (fence) and plots treated with both nutrient addition and grazer exclusion (NPK + fence).

Sampling and laboratory analyses follow the same protocol allowing direct comparison of data from all sites. Plant community composition and soil chemistry were measured at the plot level in the year prior to treatment application (Y0), and composition was measured annually at peak biomass. Community composition was determined by independently estimating the areal cover of each species to the nearest 1%. Species taxonomy was reconciled across sites and through time within a site to prevent artificial 'turnover' due to nomenclature changes through time (Lind 2016). Soil samples were collected at 0–10 cm depth. Here, we used the following soil chemistry parameters: C, N, P, K, Ca, Mg, S, Na, Zn, Mn, Fe, Cu, B and pH (Borer *et al.* 2014a). Ground level and ambient light (readings taken above the canopy around noon on a cloudless day) were also measured in each plot. Additionally, geographical parameters (latitude, longitude, elevation) were recorded for each site.

All statistical analyses were performed in R statistical computing (R Core Team 2016). For this study, we assessed how species turnover in a plot over time (temporal turnover) is affected by the initial species pool size and spatial distribution of species across all plots within one block, that is, block richness and within-block beta diversity before treatment application (Y0). We calculated block richness as the total number of plant species present in a block and within-block beta diversity as the Jaccard Dissimilarity Index (Jaccard 1912) across the 10 plots in each block ('simba' package, Jurasinski & Retzer 2012). Temporal turnover was the averaged presence–absence-based Jaccard Dissimilarity between subsequent years (Y0–Y1, Y1–Y2, Y2–Y3). We applied a presence/absence-based measure of dissimilarity and turnover, as our focus lies on species replacements which are constrained by the regional species pool, assigning equal weight to rare and common species (Anderson *et al.* 2011). We additionally separated overall temporal species turnover into two components capturing different aspects of community change. The first component represents changes in species composition resulting from species replacement ('turnover'), whereas the second component represents community richness changes caused by an imbalance between immigration and loss of species ('nestedness') (Baselga 2010; Baselga & Orme 2012). Differences in the magnitude of these two components, can reflect differing mechanisms governing compositional changes in communities (Baselga 2010). The partitioning approach is described in Baselga (2010) and calculated using the 'betapart' package (Baselga & Orme 2012). To facilitate interpretation of the two components in our temporal context, we deviated from the terminology used by Baselga (2010) and refer to the 'turnover' component as compositional changes due to species replacement (TTO_{rep}), whereas 'nestedness' will be referred to as changes in species richness (TTO_{rich}):

$$\begin{aligned} TTO_{Jac} &= TTO_{rep} + TTO_{rich} \\ &= 2 \times \min(b,c)/(2 \times \min(b,c) + a) + ((\max(b,c) \\ &\quad - \min(b,c))/(a + b + c)) \times (a/(2 \times \min(b,c) + a)), \end{aligned}$$

where overall temporal turnover TTO_{Jac} ('Jaccard') is expressed as the sum of TTO_{rep} ('replacement') and TTO_{rich} ('richness'). Here, *a* represents the number of species present in both years, *b* and *c* represent the numbers of species present in only one of the 2 years. For more details on the mathematical derivation of the above equation, see Baselga (2010). Values can range from 0 indicating no change in community composition, to 1. A TTO_{rep} of 1 indicates the complete replacement of all species in the community. TTO_{rich} is asymptotical to 1 which would indicate extinction or immigration of all species in the community.

For the estimation of spatial *environmental* variability, we calculated Euclidean distances ('vegan' package, Oksanen *et al.* 2016) for standardised soil parameters (nutrients and pH) and ambient light measurements across all plots of each block prior to initiation of treatments. To describe long-term temporal environmental variability, we standardised and aggregated variability in site-level mean annual precipitation and temperature to obtain a single measure representing climatic conditions. The data were obtained from Bioclim, which is part of a set of publicly available global climate layers at 1 km resolution (Worldclim, http://worldclim.org/bioclim).

To test our hypotheses using the specific measures described, we developed an initial structural equation model. For our first hypothesis, that environmental variability in space and/or time is a driver of pre-treatment richness and beta diversity, we incorporated pathways from the temporal (climate) and spatial (soil conditions and light) environmental variability measures to block richness and within-block beta diversity. To test our second hypothesis, that spatial heterogeneity in species composition promotes higher rates of temporal species turnover, we included pathways from within-block beta diversity to the two turnover components. Additionally, we allowed for direct effects of block richness on both aspects of temporal turnover (Allan *et al.* 2011) to account for effects of species pool size. We also included direct links between the environmental variability measures and temporal species turnover. As stated in the literature on species area relationships (Connor & McCoy 1979) and species-time-area relationships (Adler *et al.* 2005), species richness and spatial beta diversity are likely to be correlated, which also applies to our dataset. We therefore included a direct pathway from block richness to block beta diversity. Alternative model formulations and model output are provided in the supplementary material (Appendix S1.5.).

All analyses were performed using robust estimation procedures implemented in the 'lavaan' (Rosseel 2012) and 'lavaan.survey' (Oberski 2014) packages accounting for non-normality in some of the variables and the nested structure of the data (plots within blocks within sites). We ran separate SEM analyses for each treatment and the control plots and then compared estimates of the respective pathways. Soil and environmental variables were not available for all sites reducing our sample size (Ctrl: $n = 96$, NPK: $n = 95$, fence: $n = 79$, NPK + fence: $n = 80$). Model fit (Satorra-Bentler scaled Chi-square tests accounting for non-normality in the data) was assessed by calculating the deviation of the variance-covariance matrix predicted by the model from the variance-covariance matrix of the observed variables. Non-significant *P*-values indicate no detectable differences between the observed and predicted data, that is, congruence of model and observations. Additionally, several fit measures available as part of the model output in the 'lavaan' package (Appendix S1.3.) were used for model evaluation.

To test our third hypothesis, that beta diversity not only constrains annual turnover but also directional shifts in community composition in response to treatment application, we compared the community composition at the beginning of the study with the composition in the same plot after 1–5 years of treatment application. We again separated overall temporal turnover (Jaccard dissimilarity) into both turnover components (TTO_{rep}, TTO_{rich}) and tested for differences between the control and treatment plots. We fit marginal generalised linear models using the generalised estimating equations (GEE) approach from the 'geepack' package (Højsgaard *et al.* 2006) to account for the nested structure of the data.

RESULTS

Mean annual turnover varied considerably across sites ranging between 0.12 and 0.86 (Appendix S1.2.). After 4 years of treatment application, compositional dissimilarity to the control ranged from 0 to 1 (i.e. from none to complete turnover, Appendix S2.1.).

The SEM analysis yielded a significant coefficient for the path from beta diversity to the temporal turnover component reflecting species replacement (TTO_{rep}), with consistently positive effects across all treatments and the control (Fig. 1). Thus, temporal turnover by species replacement was higher when the species composition in the surrounding area was more heterogeneous. The model further revealed that plots within high richness blocks experienced less mean annual turnover in the form of replacement (TTO_{rep}) than plots in blocks with low species richness. Within grazer exclusion treatments (fence and NPK + fence), block richness was negatively associated with changes in species richness due to extinction and/or immigration (TTO_{rich}). The path coefficient between block richness and beta diversity confirmed the expected positive association between these two variables.

The model revealed a positive effect of mean annual climate (temperature and precipitation) variability on beta diversity, which was consistent across treatments. We also found a negative effect of climate variability on richness as well as significantly positive effects of spatial environmental variability on beta diversity, but only in the control and the nutrient addition plots. It should be noted that the differences in pathway significance describing effects of environmental variability on richness and beta diversity across treatments arise, in part, from the use of different data subsets. A number of high diversity sites did not apply herbivore exclusion treatments resulting in smaller sample sizes and shorter diversity gradients in the data sets including fences (Appendix S1.5.).

Overall model fit yielded *P*-values ranging from 0.30 (NPK) to 0.77 (Fence), indicating that the relationships between all variables were adequately represented by the model structure. Model fit was confirmed by further fit indices, RMSEA and residuals of the modelled and measured covariance matrices (Appendix S1.3.). For completeness, we ran SEM analyses using abundance-based turnover metrics (Appendix S1.5.). Their results corroborated the general relationships found in our presence–absence-based turnover analysis.

Mean annual turnover rates varied considerably among sites, but there was relatively little difference in the association between beta diversity and annual turnover among treatments (Fig. 2). Similarly, the linear model analysis on directional composition changes over 1–5 years revealed increasingly differing community compositions in all treatments as well as the controls (Fig. 3), and confirmed the significant effect of initial beta diversity (0.357 ± 0.106) on overall turnover independent of the type of treatment (Appendix S2.2.). However, the slope of increasing composition changes (TTO_{Jac}) was significantly stronger in the combined nutrient addition plus grazer exclusion treatment (NPK + fence) than in the control plots (0.018 ± 0.006). We further found that whereas richness changes in the control plots were similar throughout the

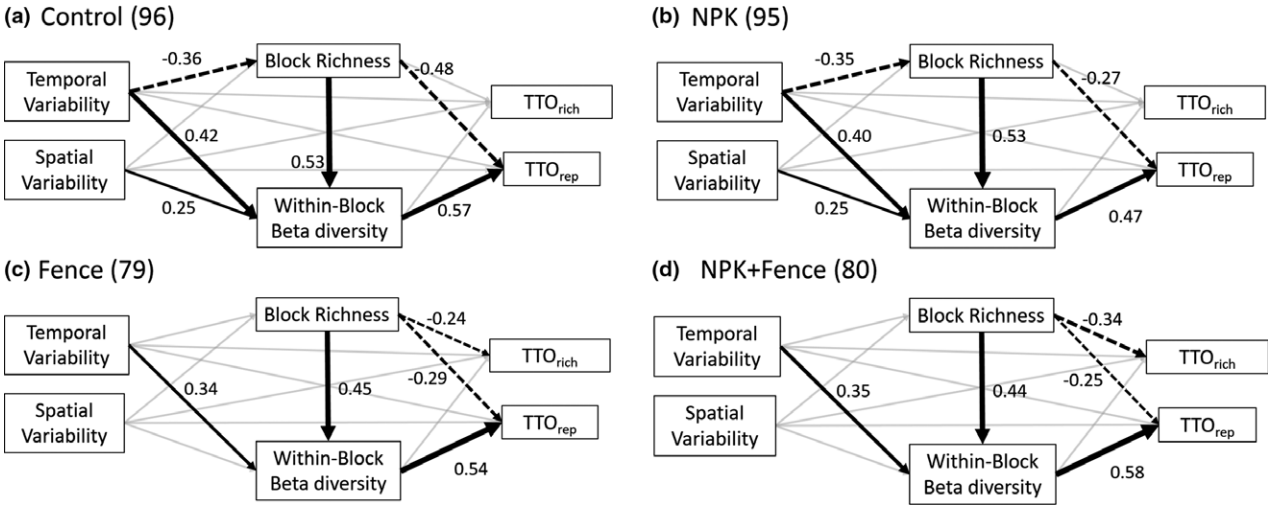

Figure 1 Structural equation model path diagram including all significant pathways in black and non-significant pathways in grey for (a) control plots, (b) nutrient addition treatment (NPK), (c) grazer exclusion treatment (Fence) and (d) combined nutrient addition and grazer exclusion treatment (NPK + Fence). The displayed estimates are standardised path coefficients. For a detailed statistical output on model fit, see Appendix S1.1.2. The width of the arrows reflect the strength of the according pathway. Line type represents positive (solid) and negative (dashed) path coefficients.

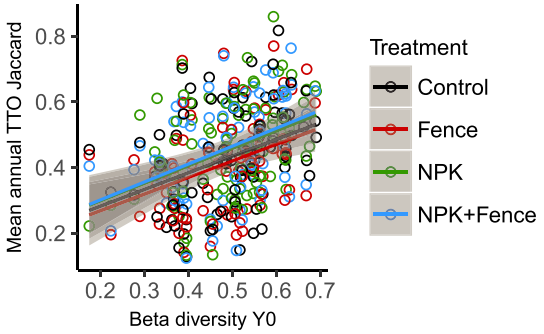

Figure 2 Relationship between block beta diversity prior to treatment application and mean annual turnover rates. The colours indicate data from control (C, black) and the three treatments grazer exclusion (F, red), nutrient addition (NPK, green) and nutrient addition plus grazer exclusion (NPK + F, blue).

study, all treated plots showed increasingly higher levels of composition change due to species loss or immigration (NPK: 0.022 ± 0.007; fence: 0.011 ± 0.005; NPK + fence: 0.025 ± 0.008). These higher levels of compositional alterations were driven by higher rates of species extinction in the fertilised plots as opposed to relatively constant numbers of immigrations, both over time and across treatments and control (see Appendix S2.3.). Compositional differences in the form of species replacement increased in all treatments and the control, but the increase was significantly less pronounced in the NPK treatment compared to the controls (−0.019 ± 0.008).

DISCUSSION

Our analysis of temporal turnover patterns in grasslands across the globe showed that the rates of compositional turnover among years were higher in plots with higher surrounding beta diversity. Additionally, fertilisation and the combined fertilisation plus fencing treatment led to a greater number of extinctions (increasing of TTO_{rich}), whereas fencing on its own resulted in similar rates of colonisation or extinction as in the control plots.

Our findings add further insights to understanding the community changes that have previously been described by Borer *et al.* (2014b). Borer *et al.* (2014b) show that species richness declined with fertilisation in the majority of sites, whereas the effects of fencing and the interaction between fencing and nutrient addition did not consistently affect richness. The latter was attributed to the effect of vertebrate consumers on light availability: richness increased with grazing if grazing enhanced light availability, but richness declined when removing grazers reduced ground-level light (Borer *et al.* 2014b). We show that the annual compositional shifts induced by fencing and fertilisation were very similar in magnitude (Fig. 3 left panel) and driven by beta diversity or site-specific conditions.

However, we also found that compositional changes differed in the magnitude of the temporal turnover components after 5 years of treatment. Fertilisation by itself led to increasing changes in species richness, but to less species turnover via species replacement (Fig. 4). In contrast, grazer exclusion resulted in values very similar to both turnover components in the control plots. Interestingly and analogous to the findings in Borer *et al.* (2014b), grazer exclusion seemed to offset the negative effect of fertilisation on species replacement in the combined NPK + fence treatment, which showed higher values of TTO_{rich} and TTO_{rep}, resulting in the observed higher overall turnover. Our results indicate that irrespective of whether species loss is caused by a reduction in niche dimensionality (Harpole & Tilman 2007) or shading effects due to increased biomass production (Hautier *et al.* 2009; Borer *et al.* 2014b), higher levels of beta diversity and larger species pools are likely to buffer fertilisation effects on community composition by mediating species loss and allowing for higher turnover.

Beta diversity enhanced species turnover rates and was positively correlated with the number of species in a block. Higher levels of block species richness, however, led to consistently lower exchange of species identities (TTO_{rep}) in all treatments. These negative correlations between richness and temporal turnover (White 2004; Shurin 2007) can result from mechanisms including limited success of colonisation and have been frequently reported in the literature (e.g. Shurin 2007;

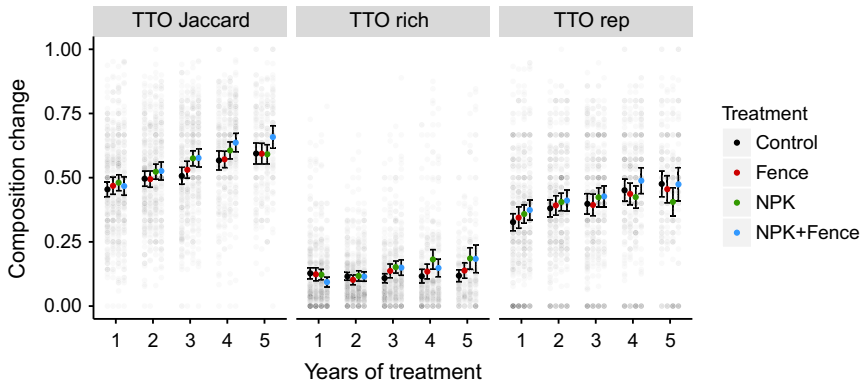

Figure 3 Composition change over time expressed as mean and standard error for overall turnover ($TTO_{Jaccard}$) and both turnover components (TTO_{rich}, TTO_{rep}) before and after 1–5 years of treatment application. The colours indicate data from control (black) and the three treatments grazer exclusion (red), nutrient addition (green) and nutrient addition plus grazer exclusion (blue). The error bars indicate 95% confidence intervals.

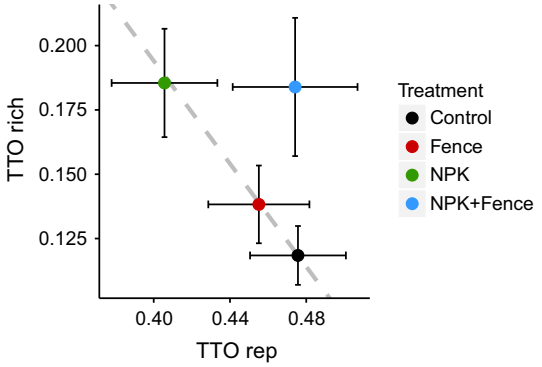

Figure 4 Composition changes in the form of species replacement (TTO_{rep}) and species richness change (TTO_{rich}) after 5 years of treatment application. The colours indicate changes in the control (black) and the three treatment plots, that is, grazer exclusion (red), nutrient addition (green) and nutrient addition plus grazer exclusion (blue). The bars represent standard errors of both turnover components. The grey line represents constant total change (Jaccard, control plots) indicating the possible paired contributions of both turnover components.

Matthews & Pomati 2012; Pandit & Kolasa 2012). Our model further indicates that climatic (temporal) and soil nutrient (spatial) heterogeneity are associated with higher beta diversity implying some level of environmental partitioning by species, which is in agreement with findings from studies spanning a wide range of ecosystems and organism types (Veech & Crist 2007; Questad & Foster 2008; García-Palacios *et al*. 2012; Heino *et al*. 2013).

Given the large amount of variance attributed to site conditions (Appendix S2.4.), beta diversity seems to be but one aspect constraining composition changes. Factors we did not take into account in our study are for instance disturbance regime, successional stage or pathogens. Investigation of site-specific conditions will be necessary to elucidate the drivers of community change in general and as a consequence of environmental change.

Our results highlight the value of integrating spatial and temporal aspects of turnover in analyses of plant community change over time, two factors that are often considered separately, although their interactive effects on turnover have been demonstrated before (Adler *et al*. 2005). Most analyses of temporal turnover in a macro-ecological context have been conducted using a within-plot perspective (Korhonen *et al*. 2010; Shade *et al*. 2013), that is, ignoring effects from outside of the experimental units. Likewise, most analyses of biodiversity change with environmental drivers have interpreted differences in the response of richness, evenness or other diversity metrics as an emergent property of the local community, not of the regional heterogeneity in diversity (Hillebrand *et al*. 2007; Murphy & Romanuk 2014). Here, we show that annual turnover and treatment-induced dissimilarity (0–100% compositional turnover after 4 years of treatment application) vary substantially across sites. While this among site variability is often attributed to different sensitivities to the environmental driver, our analyses clearly demonstrate that changes in species composition significantly increase with increasing levels of beta diversity which is in turn affected by the species pool. Thus, the variation in turnover and treatment-induced dissimilarity is caused by the sites differing in their response potential: only sites with high beta diversity provide the scope for additional species colonising the local patch when conditions change. Hence, species compositional change in response to altered environmental conditions not only depends on the strength of these alterations and the number or identity of species locally present, but also on how heterogeneously these species are distributed in space (beta diversity). These results have fundamental consequences for the analysis of compositional shifts in observational time series and in experiments that are open to colonisation: a given shift in composition (and species richness) cannot be interpreted or compared between sites without explicitly considering the spatial context, including the size of the species pool that is available for immigration. Community A might respond more to a certain driver than community B because the species in A are more sensitive to this driver, or because community A is embedded in a region with additional species being present and capable of immigration (see also Hautier *et al*. 2018).

Our analysis demonstrates that without the distinction of turnover in form of richness changes as opposed to species replacement, impacts of altered environmental conditions might be missed. Baseline turnover is an inherent property of most ecological systems (Hillebrand *et al*. 2017) and can equal overall turnover in response to environmental change, disguising significant differences in the turnover components among treatments (Fig. 4). In addition, the large proportion of the Jaccard dissimilarity explained by species replacement demonstrates that a focus on species numbers can be a very coarse measure of biodiversity change, potentially masking substantial changes in species identity and functional traits (Hillebrand *et al*. 2010, 2017; Dornelas *et al*. 2014; Jones *et al*. 2017). Our results further suggest that factors constraining turnover, such as homogenisation of environmental conditions or plot-level species richness, may also change ecosystem stability. If temporal turnover in composition is a mechanism allowing for functional stability under changing conditions (Allan *et al*. 2011; Loreau & de Mazancourt 2013; Mazancourt *et al*. 2013; Hautier *et al*. 2014), then any limitation of turnover will affect local and regional stability (Wang & Loreau 2016; Wilcox *et al*. 2017).

We provide clear evidence that spatial beta diversity at the onset of an experiment constrains the ability of a local assemblage to alter its composition over time and in response to changes in environmental conditions. Variation in response magnitudes thus may not reflect the actual impact of a change on composition, but the scope for compositional change due to the presence of additional species in the region.

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AUTHORSHIP

DH, HH, SH, EB, EL and ES conceptualised the study, DH performed statistical analyses and wrote the manuscript; all other authors contributed data and substantially contributed to revisions of the draft.

DATA ACCESSIBILITY STATEMENT

The authors agree that upon acceptance, all data supporting the results in the paper will be archived in the DRYAD data repository, https://doi.org/10.5061/dryad.8vs569h.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information section at the end of the article.

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